ON THREE MISUNDERSTOOD NEOTROPICAL SPECIES OF TECTARIA (POLYPODIACEAE: ASPLENIOIDEAE)

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ABSTRACT. A critical examination of type specimens has established that a widespread fern of southern Central America and Colombia, commonly identified as Tectaria rheosora (Baker) C. Chr., actually represents T. rivalis (Mett. ex Kuhn) C. Chr. A second widespread species, variously identified as Tectaria rheosora or T. subebenea (Christ) C. Chr., is properly T. rheosora; however, that name is here formally placed into synonymy under Tectaria athyrioides (Baker) C. Chr. Tectaria subebenea is believed to be a rare species, apparently endemic to Costa Rica. Distinguishing features and representative specimen citations are provided for each species.

INTRODUCTION

A floristic treatment of the pteridophytes of the La Selva Biological Station, Costa Rica, was recently completed (Grayum & Churchill, 1988) with the resolution of a taxonomic problem involving two of the nine species of Tectaria occurring on the property. These two species, similar in general aspect, were initially distinguished in the field at La Selva (an Atlantic lowland site), on the basis of morphological and ecological differences. Subsequently, an examination of herbarium material from throughout southern Central America and northern South America confirmed the consistency of these differences, led to the discovery of additional distinguishing features and demonstrated the widespread occurrence of both species in the general region. The existence of a serious taxonomic problem was revealed by a perusal of the specimen annotations: respected authorities frequently failed to distinguish these two species altogether, or did so inconsistently, and exhibited a general lack of consensus as to which names to use and how to apply them. Thus, the problem had both biological and nomenclatural components; the first of these aspects, as mentioned above, was resolved in the field, the second by means of a herbarium study of type specimens. Since the conclusions of this investigation are of general pertinence to Central American pteridology, they are here reported.

THE BIOLOGICAL COMPONENT: CHARACTERIZATION OF THE FERNS

The two problematical La Selva Tectaria species share the following attributes: both are moderately large ferns with stout, short-creeping to suberect rhizomes, dark petioles and frond axes, coarsely pinnate-pinnatifid to subtripinnate laminae, copiously areolate venation, free included veinlets in most areolae and indusiate sori. Both species come out to the vicinity of Tectaria rheosora (Baker) C. Chr./T. subebenea (Christ) C. Chr. in most regional keys (e. g., OTS, 1967). They may be distinguished from one another as follows:

Species A: Areolae along costae, costules and distal part of rachis with free included veinlets; lamina bipinnate to subtripinnate, usually with 4-6 pairs of free pinnae below the pinnatifid apex; petiole about equaling the lamina, dark reddish-brown to medium brown, conspicuously scaly in basal 10-20 cm; indusia regularly lunate, ciliate along the margin; primary riparian forest at La Selva, elsewhere on comparatively well-drained sites (slopes and ridges) in primary forest.

Species A ranges from the Atlantic slope of Nicaragua (or perhaps even further north) to the Pacific lowlands (Chocó) of Colombia (specimen citations for the species highlighted in this paper are provided in Appendix 1). In Costa Rica, it occurs in both the Atlantic and Pacific lowlands, mostly below 1000 m but occasionally to as high as 2250 m.

This species is regularly identified as Tectaria rheosora by most authorities. It is abundant in the canyon of the Rio Reventazón at Turrialba, Prov. Cartago, Costa Rica, and a plant from that population is illustrated under the name T. rheosora in Tryon & Tryon (1982, Fig. 69.1).

Species B: Areolae along costae, costules and distal part of rachis long, prominent, lacking free included veinlets; lamina pinnate-pinnatifid to subbipinnate (the basal pinnae simple, or with at most a single pair of free pinnules), with 2-3 pairs of free pinnae below the pinnatifid apex; petiole longer than the lamina, deep blackish-brown toward base, the scales few and restricted to the very base; indusia varying from linear to sublunate on the same frond, the margins eciliate; primary swamp forest and along sluggish portions of forest creeks.

Species B is known only from Nicaragua (Matagalpa) to Panama (Veraguas), from sea level to about 1100 m. Collections have been seen only from the Atlantic slope.

This species is identified either as Tectaria rheosora or, about equally as often, T. subebenea; a few authors have annotated specimens as "Tectaria sp. nov."

NOMENCLATURAL CONCLUSIONS

A recent visit to the herbarium of the Royal Botanic Gardens, Kew, England (K), afforded the opportunity to examine all of the type specimens relevant to the problem under discussion (as well as several others that proved to be irrelevant). Coming hard on the heels of extensive field and herbarium experience with this group of ferns, the interpretation of these types was straightforward and, in fact, instantaneous, leading to the following three principal conclusions:

1. Species A, surprisingly enough, is neither Tectaria rheosora nor T. subebenea but, rather, Tectaria rivalis (Mett. ex Kuhn) C. Chr. Both isosyntypes of Aspidium rivale Mett. ex Kuhn, the basionym, were studied at K: Seemann s. n. (January, 1848), from the Bay of Utria, Chocó, Colombia; and Fendler 406, from Chagres, Panama. The Seemann specimen is an isolectotype, Seemann s. n. (US) having been selected as the hololectotype by Lellinger (1977). The latter author states that the Fendler collection is actually Tectaria rheosora, based on an examination of a photograph of the holosyntype at B. Although I have not seen Fendler 406 (B), the isosyntype at K is clearly not T. rheosora; it differs only negligibly (i. e., in pubescence of the frond axes) from the Seemann specimen and, like Mettenius, I regard the two collections as conspecific.

2. Species B corresponds to Tectaria rheosora (Baker) C. Chr.; the holotype (Harrison 54, Costa Rica) of the basionym, Polypodium rheosorum Baker, is a single, unusually small leaf, however there is no question that it represents this entity. But there is a complication here: the type of Nephrodium athyrioides Baker, the basionym of Tectaria athyrioides (Baker) C. Chr., also represents Species B. Priority cannot be invoked to select the correct name, since both basionyms were published in the same article by Baker (1884); moreover, both new combinations in Tectaria were made at the same time (Christensen, 1934).

History has treated these two names very differently, however, in terms of their usage in botanical literature and in herbaria. Nephrodium athyrioides literally passed into oblivion as soon as it was published. Except for the occasion of its formal transferral to Tectaria, I have been unable to find any mention of the name in the literature, nor have I seen any herbarium specimens so identified. But although the name is not used, neither does it appear to have been listed in synonymy under another name.

Tectaria rheosora, on the other hand, has become a well known name--but for all the wrong reasons. It has been consistently misapplied to the wrong species, especially T. rivalis, while many collections legitimately entitled to the name have been identified as T. subebenea.

The above patterns appear to have become entrenched at a very

early date. For example, Bommer & Christ (1896) made absolutely no mention of Nephrodium athyrioides (although the type is from Costa Rica), while under Polypodium rheosorum they cited at least one specimen of Tectaria rivalis. Later authors have merely followed suit.

In spite of its familiarity, the name Tectaria rheosora (Baker) C. Chr. is here formally placed into synonymy under T. athyrioides (Baker) C. Chr. for the purposes of the La Selva flora. As far as I am able to determine, this action establishes a precedent in this regard. The decision is justified as follows: first, the type of Nephrodium athyrioides is a better and more representative specimen than that of Polypodium rheosorum (in fact, it consists of two sheets; since these are differently numbered, one is here arbitrarily designated as the lectotype). Indeed, the type specimen of P. rheosorum was actually misinterpreted by the author of the name, as noted on the sheet by Prof. R. E. Holttum (14.12.1981): "I see no distinction between this and Tectaria athyrioides (Bak.). Indusia are present, not seen by Baker." It was Baker's failure to discern indusia on this specimen that caused him to assign it to Polypodium, rather than Nephrodium; the indusia are clearly evident on the type of N. athyrioides.

A second reason for preferring Tectaria athyrioides over T. rheosora is that Baker later illegally reused the name Polypodium rheosorum for an unrelated, Chinese species (Baker, 1891). This is perhaps rather minor, but adds to the general aura of confusion that has attended the epithet since its publication. It can safely be said that the name Tectaria rheosora has never been correctly and consistently applied to the species represented by the holotype, by any authority. Now that this species is well understood and has been clearly characterized apparently for the first time, it seems well to start it on its way with an untarnished (if little known) name. A complete synonymy follows:

Tectaria athyrioides (Baker) C. Chr., Index filicum, suppl. III:177. 1934. Nephrodium athyrioides Baker, J. Bot. 22:363. 1884. Aspidium costaricanum C. Chr. (not A. athyrioides Mart. & Gal. 1842), Index filicum, fasc. II:70. 1905. TYPE: COSTA RICA, Harrison 30 (lectotype: K).

Tectaria rheosora (Baker) C. Chr., Index filicum, suppl. III:184. 1934. Polypodium rheosorum Baker, J. Bot. 22:363. 1884 (not 1891). Aspidium rheosorum (Baker) C. Chr., Index filicum, fasc. II:90. 1905. TYPE: COSTA RICA, Harrison 54 (holotype: K).

3. Tectaria subebenea (Christ) C. Chr. appears to be a distinctly different species from the two previously discussed, and is not represented at La Selva. It agrees in general with T. rivalis and T. athyrioides in having large, pinnately divided fronds with areolate venation; the indusia are round and ciliate, and there are some (but few) free included veinlets in the costal areolae.

T. subebenea differs in its larger fronds, even darker (nearly black) frond axes and, most strikingly, in its broadly ovate, hyaline petiolar scales. Although I do not know this species in the field, I feel confident that it is a separate entity (the point is moot with respect to the problems discussed in the preceding sections, Aspidium subebeneum Christ being the most recent of any of the basicnyms involved). Judging from the available specimens, Tectaria subebenea is endemic to Costa Rica, where it occurs from about 200-1400 m.

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APPENDIX 1

REPRESENTATIVE SPECIMENS EXAMINED

Tectaria athyrioides (Baker) C. Chr.

COSTA RICA. No other location, Harrison 30 (lectotype, K), 31 (syntype, K), 54 (holotype of Polypodium rheosorum Baker, K). ALAJUELA: Burger & Stolze 4940, 5051 (CR). HEREDIA: Biolley 7497 (CR), Burger & Burger 8046B (CR), Chacón 537 (CR), Grayum 8289 (CR, MO), Grayum & Chavarria 8293 (CR, MO), Hammel 10372 (CR, DUKE), McDowell 765, 1068 (CR, DUKE), Pittier 7497 (BR), Scamman 7470 (CR), Smith et al. 1781 (CR, UC). SAN JOSE: Biolley s. n., 7/1888 (M), Kupper 350 (M), Pittier 666, 1181 (BR).

NICARAGUA. MATAGALPA: Araquistain & Moreno 2652 (CR), Neill 1806 (CR). ZELAYA: Neill 1851 (CR).

Tectaria rivalis (Mett. ex Kuhn) C. Chr.

COLOMBIA. CHOCO: Seemann s. n., 1/1848 (isolectotype; K).

COSTA RICA. ALAJUELA: Croat 36519 (CR, MO), Lellinger & White 1640 (CR). CARTAGO: Grayum & Hammel 5740 (CR, MO), Skutch 4618 (CR). HEREDIA: Grayum 2707, 3045 (CR, DUKE), 8288 (CR, MO). LIMON: Antonio 607 (CR), Croat 43207 (CR, MO), Grayum et al. 7688 (CR, MO), Moran 3094, 3122 (CR), Pittier 3099, 6804 (CR), Tonduz 9484 (CR). PUNTARENAS: Burger & Gentry 8924 (CR), Burger & Liesner 7258 (CR), Utley & Utley 1091, 1188 (CR).

NICARAGUA. RIO SAN JUAN: Neill 3410 (CR). ZELAYA: Stevens 6313 (CR, MO), Vincelli 135, 219 (CR).

PANAMA. CANAL ZONE: Fendler 406 (isosyntype; K). PANAMA: Hamilton et al. 3241 (CR, MO). VERAGUAS: Antonio 2371 (CR, MO).

Tectaria subebenea (Christ) C. Chr.

COSTA RICA. No other location, Endres s. n. (K). ALAJUELA: Croat 43620 (CR, MO). LIMON: Tonduz 9447 (type; CR, K). PUNTARENAS: Anonymous (McAlpin?) 74-1173 (CR-57978). SAN JOSE: Valerio 33480 (CR).